

groups, but generally there appears to be considerable variability even within the species in such particulars as the size of the flowers, the number in the corymbs and the compactness or laxity of the latter. The shape of the leaves is even less stable and dependable, many types often being found on a single branch. . . . The fruit is often one of the best guides to group distinctions, but there is quite too much variation in such particulars as shape, size and color for them to be depended upon rigidly as specific criteria. . . . Even the presence or absence of pubescence on the corymbs, often one of the best specific distinctions, cannot always be relied upon." The number of stamens and color of anthers are considered one of the most definite criteria for distinguishing species, but stamen number is also variable and anther color is often correlated with the color of the fruit.

Seedlings of the more ornamental types have been grown in considerable numbers at Rochester Park and at the Arnold Arboretum. My colleague, Mr. E. J. Palmer, informs me that in most cases the species of *Crataegus* breed true from seed, even to the most minute characters. Many species have a wide geographic range while others are of very local geographic distribution.

Longley has investigated about 80 species of *Crataegus* and found that about three-fourths of these species are triploids. Standish (1916) found that pollen sterility was prevalent in about 80 per cent of the species studied and in many cases pollen sterility was complete. It seems probable then that about 75 per cent of the *Crataegi* are triploids and form partially or completely sterile pollen. In view of the prevalence of triploids and pollen sterility in this genus it is remarkable that almost all species of *Crataegus* produce fruits abundantly. And still more remarkable some of these triploid forms with partially sterile pollen are known to breed true from seed. The only explanation of these phenomena seems to be that the triploid species are apogamous, or that seeds develop, from unreduced egg cells, so that the progeny receive the maternal set of somatic chromosomes and would of course breed true.

This explanation of seed production in the triploid *Crataegi* will account for the numerous species found in this genus. It is quite probable that there are at least several distinct types of *Crataegi* whose chromosomes are completely differentiated, but for the most part the different forms have similar basic sets of chromosomes. Variations caused by mutation and by hybridization between similar types which differed in such characters as size and color of fruit, pubescent or glabrous corymbs, color and number of anthers and leaf shape would produce many different types of segregates

differing only in these minor characters. The occasional production of diploid gametes, which seems to be characteristic of many genera of the Rosaceae, would frequently result in the production of triploids. These triploids seem to have developed a type of apogamous reproduction so that they breed true for both morphological characters and chromosome number. The older triploid types would be expected to have as great a geographic range as the diploids but the more recent ones would have only a local range.

Triploids could also be derived from homozygous diploids and from crosses between diploids and tetraploids. The production of triploid forms from diploid species will cause chromosome irregularity and pollen sterility, so that these phenomena are not necessarily associated with hybridity. Chromosome irregularity can also be caused by genetic factors, grafting, X-rays, segmental interchange between non-homologous chromosomes, and to some extent by environmental conditions.

There is also some evidence for apogamy in the genus *Malus* (Kobel 1927). Mr. W.H. Judd of the Arnold Arboretum tells me that some of the *Malus* species breed true from seed. In the Arboretum a number of species are grouped together and in many cases a species is represented by a single tree. In view of the fact that all horticultural varieties of *Malus* are cross pollinated, it is remarkable that any of the species grown in the Arboretum should breed true, unless they develop seed by apogamy or from unreduced egg cells. Certainly the cultivated varieties do not breed true from seed. In connection with some breeding experiments a number of flowers of *Malus theifera* were emasculated while the anthers were green and before the buds opened. The stigmas were also cut off at the same time and yet most of the fruits developed to maturity and seeds were obtained. Thus there are several lines of evidence that some species of *Malus* are apogamous or parthenogenetic, but further work should be done with both *Crataegus* and *Malus*.

In view of the close relationships of many genera of the Pomoideae and the frequency of fertile species hybrids in most genera the validity of the taxonomic grouping must be questioned. Of course the differentiation of species limits is a matter of personal opinion as best indicated perhaps by the recognition of about 5000 species of *Rosa* by some taxonomists as compared with 100 to 200 recognized by Rehder.

There should be a specific genetic test to determine species relationships. The use of the term species as used by most taxonomists seems to be almost as indefinite as it was in Darwin's time. From the standpoint of genetics and cytology a species might be defined as

a group of individuals of common descent which possess genetically similar sets of chromosomes. Such a definition will have to be modified at times in view of occasional genetic factors which may inhibit hybridization and affect the fertility of hybrids even in varietal crosses, but it is fundamentally sound. Of course such a test of genetics and cytological relationships can be applied only to a limited extent, but it should provide a more precise and natural system of classification for many groups of plants.

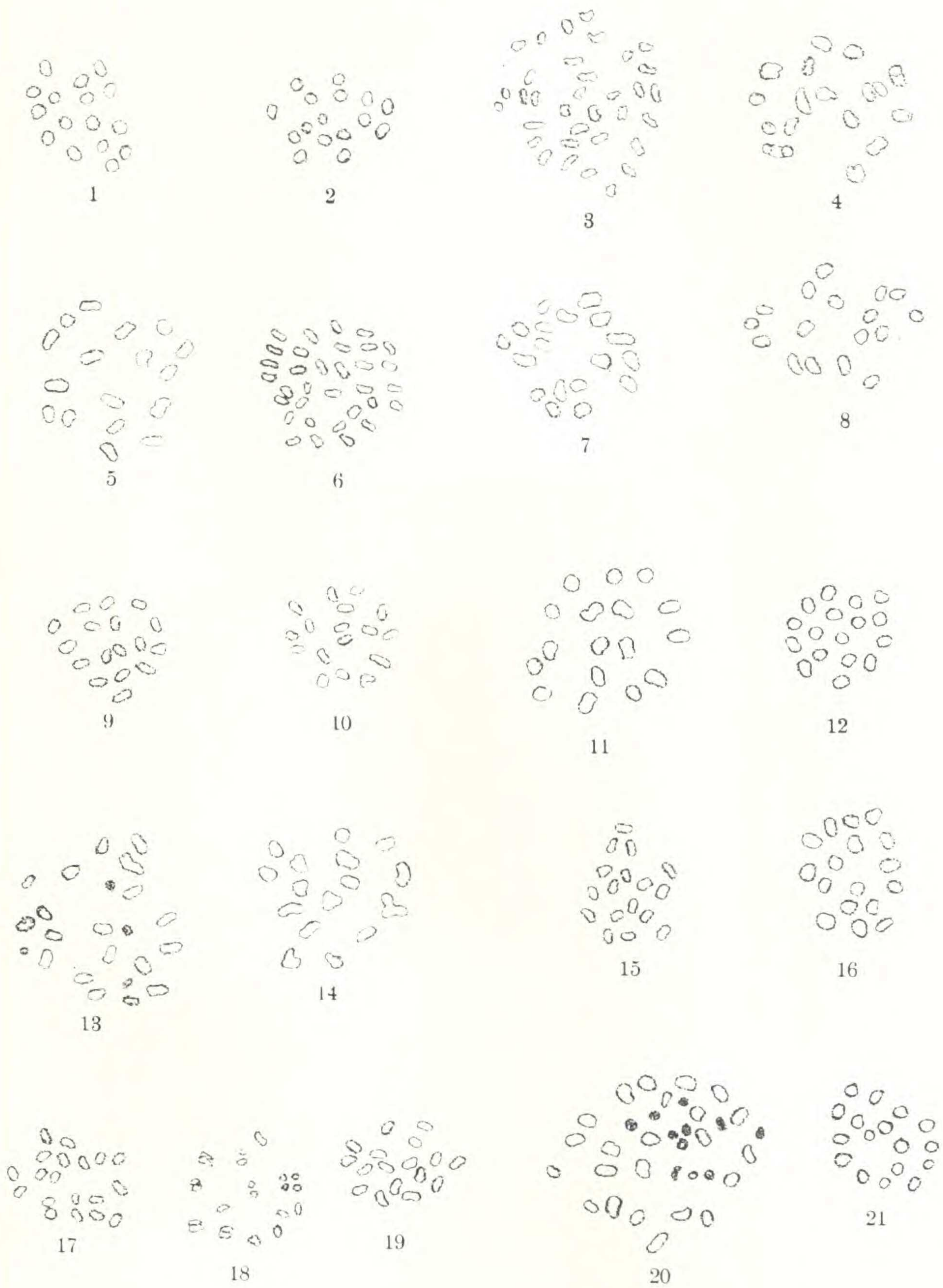
According to the genetic system of classification perhaps all of the Pomoideae could be classed as one genus and most of the present genera could be regarded as genetic species. In some cases two different genera, such as *Sorbus* and *Aronia*, should be combined in one genetic species. In the larger genera it is quite probable that there are a number of good genetic species so that the number of genetic species would exceed the present number of genera. This reversion to the older system of classification of the Pomoideae seems to be more in accord with genetic relationships than the present system, although a considerable amount of work must be done to determine the relationships of all of the genera and species.

#### SUMMARY.

In the Rosaceae the basic chromosome number is 8 and 9 for the Spiraeoideae, 7 and 8 for the Rosoideae, 8 for the Prunoideae, but is 17 for the Pomoideae. In the Rosoideae and Prunoideae, and probably in the Spiraeoideae, the larger genera include a series of polyploid species. In several genera which have been extensively studied it has been shown that species differentiation is caused by genetic differentiation of basic sets of chromosomes and by hybridization associated with polyploidy.

In the Pomoideae a few of the larger genera contain many triploids and a few tetraploids, but these forms are probably autopolyploids. The genera of Pomoideae have apparently had a common origin and have developed by genetic differentiation within the basic set of 17 chromosomes.

Many of the genera of Pomoideae are very closely related. *Sorbus* and *Aronia* have similar sets of chromosomes which pair in  $F_1$  hybrids. Generic hybrids are also known to occur between *Crataegus* and *Mespilus*, *Sorbus* and *Amelanchier*, *Sorbus* and *Pyrus*, and *Pyrus* and *Cydonia*. Other genera are morphologically very similar although no generic hybrids are known to exist. The species in the larger genera are often closely related and natural species hybrids are commonly found.



ORIGIN OF POMOIDEAE

On a genetic and cytological basis of classification all of the present genera of the Pomoideae might be classed as genetic species under one genus. In at least one case two genera should be combined in one species.

Most of the numerous species of *Crataegi* are triploids and are fruitful and breed true apparently due to apogamy or parthenogenesis. Most of these triploid forms are probably the result of polyploidy within a genetic species and should be classed as varieties which breed true by asexual reproduction.

There is some evidence of secondary chromosome association at meiosis which may indicate that the present diploid genera are polyploids with an original basic chromosome number of 7 or 8.

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#### DESCRIPTION OF PLATE 28

From acetocarmine preparations of pollen mother cells.

- Figure 1. *Crataegus Lavalleyi*. First metaphase.  
 2. *Mespilus germanica*. First metaphase.  
 3. *Cotoneaster horizontalis*. Second metaphase.  
 4. *Cotoneaster moupinensis*. Diakinesis.  
 5. *Sorbus Aucuparia*. First metaphase.  
 6. *Crataegus lawrencensis*. Telophase.  
 7. *Crataegus lawrencensis*. First metaphase.  
 8. *Crataegus Deweyana*. Late diakinesis.  
 9. *Chaenomeles sinensis*. Second metaphase.  
 10. *Photinia villosa*. Second metaphase.  
 11. *Aronia melanocarpa*. First metaphase.  
 12. *Sorbus alnifolia*. First metaphase.  
 13. *Crataegomespilus grandiflora*. Late diakinesis.  
 14. *Crataegomespilus grandiflora*. First metaphase.  
 15. *Crataegomespilus Dardari*. First metaphase.  
 16. *Amelanchier oblongifolia*. First metaphase.  
 17-19. *Sorbopyrus auricularis bulbiformis*. Telophase.  
 20. *Sorbopyrus auricularis bulbiformis*. First metaphase.  
 21. *Sorbaronia Dippelii*. First telophase.

The bivalents have divided and are shown at each pole in figures 17 and 19, while the lagging univalents are shown in figure 18.

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## CYTOMYXIS

ROBERT H. WOODWORTH

WHILE making a study of pollen development in *Oenothera gigas* and *O. biennis*, Gates (3) frequently noted an extrusion of chromatin from the nucleus of one pollen mother-cell across plasma strands into the cytoplasm of an adjacent mother-cell. He considered this to be a normal process and called it cytomyxis. Since that time thirty or more cytologists have observed and reported these cytoplasmic strands and chromatic extrusions. A few of the early students considered the process to be normal.

Rosenberg working with *Drosera* (5), Sakamura with *Vicia* (6), Sinoto on *Iris* (7), Yasui with *Papaver* (10), Tischler with *Phragmites* (8), and Erlanson on *Rosa* (2) all think of this nuclear behavior as extremely abnormal and variously suggest that it is due to faulty technique in handling living material, to the action of the fixing fluids or even to pathological conditions. The present tendency has been to agree with the one or other explanation.

Several recent workers (Hicks 4, Church 1, Woodworth 9) who have been studying plant groups mainly from the standpoint of chromosome numbers and abnormalities of the reduction division with a view to detecting plants of hybrid origin, have paid some attention to cytomyxis especially when it involves chromosomes, chromosome groups, and even whole spindles. If such a transposition of chromosomes be normal and the cells in question could function in fertilization, the chromosome number in the gamete would be other than haploid. This would be of some genetic significance. It was thought to be important enough to stimulate further consideration of the normality or abnormality of cytomyxis.

Professor K. Sax has obtained some pertinent data concerning the nature of cytomyxis from a study of smear preparations of pollen mother-cells of *Secale* and other plants. Rye is especially good for such studies because if the end of the anther is cut off the pollen mother-cells may be squeezed out with little change in the normal arrangement of the cells. When such preparations are fixed and stained with aceto-carmin, or fixed in the usual fixatives and stained with crystal violet and iodine, there is little evidence of cytomyxis except at the late spireme stage. The spireme stages do show as high as ten per cent of the cells with chromatin connections but these cases are usually confined to the ends of the string of pollen mother-cells where the anther was cut or where it was pressed in removing the contents. At diakinesis one may occasionally find one or more bivalents which have passed into adjacent cells. At

metaphase and later stages there is no evidence of chromosome migration and the normal chromosome number and arrangement is found in practically all cells.

When the pollen mother-cells are squeezed out of the anther with enough pressure, or smeared with a flat needle after their removal from the anther so that the string of cells is flattened on the slide, "cytomyxis" is found very frequently. In fact under such conditions it is often difficult to find normal spireme stages. Most of the pollen mother-cells have distorted nuclei and chromatic strands between adjacent cells. This may also obtain at diakinesis when chromosomes are extruded into the cytoplasm, into adjacent cells, or into the fixing fluid where they are lost.

Some three hundred slides of the betulaceous catkins which were prepared and studied for chromosome numbers and peculiar behavior (Woodworth 9) were reëxamined for cytomyxis. The anthers which showed this protoplasmic continuity were usually in groups while the surrounding stamens, by far the majority in the catkins, showed no cytomyxis whatever. These aggregations of cytomyctic anthers appeared to be located either where the catkins were held between the thumb and forefinger when their sides were sliced off preparatory to dropping them into the fixing fluid or at a region where the razor blade passed through. The catkins were certainly not handled roughly but it seems that roughness of handling is a relative matter and that the pressure of holding and cutting the catkins must have caused the delicate mother-cells to expel some of their contents. The action of the fixative might contribute to these abnormalities initiated by pressure.

The above conclusion is substantiated by the fact that many species of *Betula* which showed cytomyxis have quite normal meiosis producing perfect pollen. If extrusion of chromatin, especially chromosomes, from one cell into another were a normal process it might reasonably be expected that the pollen grains would be varisized or even sterile in part.

As a check to the foregoing conclusion catkins of some of the species which showed cytomyxis were collected with great care to avoid pressure. These were imbedded and when sectioned showed almost no cytomyxis.

Hybrid plants which have considerable irregularity in the reduction division show the most extreme cases of cytomyxis wherein chromosomes and sometimes even spindles are transposed into adjacent cells. It would seem that some innate unbalance in the heterozygous protoplasm makes it much more susceptible to even slight pressures which would cause the extrusion of chromosomes.



Those students who have seen cytomyxis in the mother-cells of species of plants have not noted the subsequent phases of meiosis to have a deficiency or excess in the chromosome number of any of the cells as an effect of chromosome migration. The evidence now at hand strongly indicates that cytomyxis is not a natural process. Injury to the cells by pressure at the time of preservation seems to account for these cytoplasmic connections and chromatic extrusions.

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### STUDIES IN GANODERMA

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*Plates 29 and 30 and Text figure*

#### INTRODUCTION

AMONG my field collections made in the summer of 1929 is a specimen of a *Ganoderma* from a fallen Spruce on an island in Remi Lake, northern Ontario. It is a normal fructification, annual, heavily laccate or varnished above, smooth and shining, rich reddish brown in color, laterally and rather stoutly stipitate. The stipe broadens at its apex, without demarcation, into the pileus; and both are alike in the characters just noted. The context is punky and rather tough, creamy white throughout, except close to the pores,

where it darkens to chocolate brown. The pore layer is uniformly brown. The spores are abundant, and have the wall structure which is characteristic of *Ganoderma*, that is, a smooth and comparatively light epispore, and a dark, thick-walled, echinulate endospore. Apart from the fact that the fungus was growing on Spruce, it would seem to be *Ganoderma lucidum* according to Karsten, or *G. Tsugae* according to Murrill, but which, if either?

Having access to Professor J. H. Faull's collection at the Arnold Arboretum, I found almost identical specimens on Hemlock, Birches, and Oaks from America, and on *Abies* from Europe. I also found there others of curious interest, stalked and sessile *Ganodermas*, annuals and a few perennials, and some taken from the bases of living trees in which the fungus was evidently the cause of a butt rot. My aroused curiosity led me also to examine the copious American collections largely assembled by Dr. W. A. Murrill in the herbarium of the New York Botanical Garden, and the collections especially rich in old world material in the Farlow Herbarium of Harvard University.

One would naturally expect substantial agreement among authorities on the Polyporaceae as to the diagnostic criteria on which the definitions of the commoner north temperate zone species of *Ganoderma* are based. Representative specimens are frequent, they are conspicuous, they carry prolific crops of spores which are available at all times, and they are among the first to find a place in almost every mycological herbarium. One would expect to be able to determine quickly and unerringly the name of such a specimen as the Remi Lake plant from any good manual or paper dealing with the group to which it belongs, but such is not the case.

According to the European manuals this specimen would be referred to *Ganoderma lucidum*. There is not, however, the same unanimity among American authorities. Murrill in his presentation in the North American Flora (12) does not recognize *G. lucidum* as occurring in North America. What appears to be the same thing as the Remi Lake plant is described there under the name *G. Tsugae*, and no other description is applicable. But he affirms that *G. Tsugae* is restricted to Hemlock; while this plant was on Spruce, two hundred miles north of the range of Hemlock. If we consult Atkinson's paper on *Polyporus lucidus* (2) we find closer agreement with the European mycologists; to him it would be *G. lucidum*, though in the matter of nomenclature he prefers the name *G. pseudoboletum*. To Atkinson *G. Tsugae* is not a distinct species. Overholts, in his "Comparative Studies in the Polyporaceae" (15) agrees with neither Atkinson nor Murrill. He does accept *G. Tsugae*

as a good species, under the name *Polyporus Tsugae*, extending the host range to include Pine; but he also recognizes *G. lucidum* under the name *P. lucidus*, in our flora. The latter, however, he finds on hardwoods only. He appears to take no cognizance of the fact that *G. lucidum* in Europe is not so restricted; and *G. lucidum*, as he sees it, is made to include an entirely different plant described by Murrill as *G. sessile*. If we follow Overholts, the decision between *G. Tsugae* and *G. lucidum* rests predominantly on the host, that is, whether it be a conifer or a hardwood.

This instance serves as an example of the confusion that exists with respect to conceptions of species of *Ganoderma*, especially in the American flora. Moreover, confusion exists with respect to not only the species, but also the genus itself. A short excursion into the literature soon reveals the fact that the *Ganoderma* of one author is not the *Ganoderma* of another. Interest, therefore, naturally expanded from a diagnosis of the Remi Lake specimen, to the making of a broader survey of the subject, and to the undertaking of more intimate studies. The results are presented in this paper; they include a review of the taxonomic history of the genus *Ganoderma*, a presentation of definitions of what are believed to be some of the valid species in our flora, and an account of the studies on which these definitions are based.

## HISTORICAL

### 1. THE GENUS GANODERMA.

The genus *Ganoderma* was established by Karsten in 1881. In an earlier (1876) systematic work (8), following the Friesian classification of the Polyporaceae, Karsten treated the form which was later to be *Ganoderma lucidum* as *Polyporus lucidus*, the species coming within the Friesian sub-genus *Pleuropus*, which included forms laterally or eccentrically stipitate. The characteristic varnishing was noted in the specific description. In his (9) "Enumeratio Boletinearum et Polyporearum Fennicum Systemate novo dispositarum" (1881) the new genus, *Ganoderma*, was instituted. The author's conception of it was conveyed rather briefly in a key to the Polypores, and was essentially as follows, translated from the original Latin: "Context white, at times golden yellow, or rarely rose or clay colored. Spores white. [Sporae (omnium?) albae]. Pileus flexible, corky, leathery, or woody. Pileus stipitate. *Ganoderma* n. gen. Pileus and stipe laccate." Only one species, namely *G. lucidum*, was described. Later, in his "Critical Review of the Basidiomycetes of Finland," (1889), Karsten continued to recognize *Ganoderma*, and for the first time gave as synonyms the

“*Polyporus* of other authors in part” and “*Placodes* of Quélet, in part.”

It should be explained that *Placodes* as defined by Quélet, (18) comprised woody, persistent forms, with encrusted, sulcate pilei, which in the main are sessile but not infrequently resupinate, or rarely with a tuberculate stipe. Quélet placed *P. lucidus* in an apparently more or less aberrant section of the genus, comprising corky forms with a thinly encrusted surface, colored context, and dark spores. The species was described as having the pileus and stipe “varnished.” Quélet’s *Placodes* was made by him to include such diverse species as *Polyporus betulinus*, *Fomes applanatus*, and *F. fomentarius*.

It seems probable that Karsten, referring to “*Placodes* in part” as synonymous with *Ganoderma*, had in mind Quélet’s section “*Suberosi*,” and in particular that part of it reserved for species with colored spores, in which, to be sure, only *P. lucidus* is found. We must also conclude that subsequent to the time of his earlier work in 1881 when the genus was established, Karsten had become impressed with the peculiar character of the spores of *G. lucidum*, with the result that in his work of 1889, to which reference is made above, he based his description of the genus on spore characters, and did not refer to the varnishing of the pileus and stipe which earlier had been the generic criterion. Hence we are in some doubt as to the essential criteria of *Ganoderma* as conceived by Karsten, and this uncertainty has at least contributed to the difficulties in interpreting the genus which others have experienced in working with forms representative of a much wider geographical range.

This leads us naturally to a consideration of the work of Patouillard, whose collections were representative of a much wider field. Karsten confined himself solely to temperate Europe, while Patouillard gave his attention to tropical collections as well. In his study “*Le Genre Ganoderma*” (17), which appeared the same year as Karsten’s later studies of the Polyporaceae of Finland, Patouillard emphasized the importance of spore characters in the study of the taxonomy of the Polypores. He referred to Karsten’s original definition of the genus *Ganoderma*, but considered that there were many forms other than *G. lucidum*, which, chiefly on the evidence of similar spore structure, properly belonged in the same group. Patouillard included in the genus those forms characterized by a more or less colored context, and a rigid brittle crust which is more or less shiny, either smooth or rimose and formed of thickened hyphal elements. The spores of the included species are brown or yellowish, ovoid to globose, either smooth or asperulate, and some-

times with thickened or cuticularized walls. He also stated that some of the forms are annual, while others are persistent, and that they may be sessile or stipitate. Patouillard described about 50 species, which were sub-divided into two groups—the first, sub-genus *Ganoderma* vrai, having ovoid spores, and sporophores with a shiny, well varnished crust; and the second, which is composed of tropical and sub-tropical species, sub-genus *Amauroderma*, having globular to subglobular spores, and sporophores with little if any surface varnishing. Thus through his desire to include in the genus *Ganoderma* all those species which have one, or both of the characters of varnishing and “rough” spores, Patouillard was led to extend its bounds much beyond what we must consider to have been the original conception of the genus.

Turning to American authorities, we find that Murrill gives the essential character of *Ganoderma* simply as a reddish brown varnishing of the surface of the sporophore, thus holding rather closely to Karsten's original description. In his treatment in North American Flora, he makes a new genus of Patouillard's sub-genus *Amauroderma*, to include epixylous, stipitate, encrusted, but not varnished forms, with ovoid to globular brown spores. The species in North America are confined to the tropics or sub-tropics.

Miss Ames (1) follows somewhat the treatment of Patouillard. Her conception of the genus is broad. Its essential characters are a fruit body with a heavily encrusted upper surface, which might be either of the “palisade” type noted by Patouillard, as in *G. lucidum*, or of the “interwoven” type as in *Fomes applanatus*. Varnishing is not considered an essential character. The spores must be smooth, pale to dark brown, with a “wall perforated with darker lines”—a description which was derived from Atkinson's account, based on his careful observations, of the structure of the spore. Inconsistently, Miss Ames includes such species as *Fomes fomentarius*, which we now know possess spores with simple, smooth walls. Presumably, with regard to such, she had not seen their spores, and mistakenly assumed that they were of the *Ganoderma* type.

For the sake of easier comparison of the criteria of *Ganoderma* as conceived by the several authors who have treated the genus, the essentials of their descriptions are arranged in tabular form on page 30:

## DESCRIPTIONS OF GANODERMA

Author	Habit	Persistence	Context	Crust		Spores
				Surface	Structure	
Karsten* †	stipitate	— —	— —	varnished	— —	— — ovoid, warty, yellow-brown
Patouillard	stipitate or sessile	annual or perennial	—	brittle, shiny, smooth or rimose	formed of thickened hyphal elements	ovoid to glo- bose, yellow or brown, smooth or asperulate
Murrill	stipitate or sessile	annual or perennial	brown or pallid	varnished red or brown	—	ovoid, brown
Ames	stipitate or sessile	annual or perennial	fibrous to corky or woody; pale to dark brown	hard, sometimes varnished	—	smooth, wall perforated with darker lines; pale to dark brown

\* Karsten 1881.

† Karsten 1889.

## 2. TAXONOMIC HISTORY OF CERTAIN SPECIES

(a) *Ganoderma lucidum* (Leys.) Karst.

The synonymy of *Ganoderma lucidum* (Leys.) Karst. is recorded by Atkinson (2) under *G. pseudoboletus* (Jacq.) Murrill quoted incorrectly by him as *G. pseudoboletum* as follows:

*Agaricus pseudoboletus* Jacquin, Flor. Aust. 1: 26-27. pl. 41 (1773).

*Boletus rugpsus* Jacquin, Flor. Aust. 2: 44. pl. 169 (1774).

*Boletus obliquatus* Bulliard, Herb. France, pl. 7 (1780).

*Boletus lucidus* Leysser, Flor. Halensis. 300 (1783).

*Polyporus lucidus* Fries, Syst. Myc. 1: 353 (1821).

*Polyporus laccatus* Persoon, Myc. Eur. 2: 54 (1825).

*Ganoderma lucidum* (Leys.) Karsten, Rev. Myc. 3: no. 9, p. 17 (1881).

*Ganoderma Tsugae* Murrill in Torr. Bot. Club, 29: 601 (1902).

It was on a specimen of this form that Karsten based the genus. The distinctive fructifications had long been recognized throughout Europe and occur there commonly. All the European descriptions allow for considerable variation in habit, shape, color, and also host range. Thus Fries (6) describes *Polyporus lucidus* as with or without stipe, the position being central, eccentric, or lateral,—in which case the pileus is reniform. The color is light yellow when young, chestnut or almost black when mature. The occurrence is on the trunks of Oaks and other trees in Europe, Asia, Japan, and North America. In the Exsicc. Karst. Fung. Fenn. 1865, no. 239, *Polyporus lucidus* Leys. is reported as occurring on *Quercus*, *Alnus*

*glutinosa*, and *Abies excelsa*. In Krieger's collection there is a specimen from Birch. Others have collected it from Willow, and as Karsten himself reports, specimens have been collected from conifers.

While European taxonomists are substantially in agreement on *Ganoderma lucidum* in Europe, American authorities on the other hand hold very diverse views of the species, both as to host relationships and morphological characters. There are three prevailing American conceptions as represented by Atkinson, Murrill, and Overholts.

Considering host relationships first, Atkinson holds that *Ganoderma lucidum* occurs in the American flora, but he surmises that there are various strains of the species both here and in Europe. From first hand observations, he holds that there are two distinct strains in Europe. He calls attention to a very dark form on Firs in the Jura mountains, and to a lighter form on the other hosts. The latter he designates as *G. pseudoboletum typicum*, and the former as *G. pseudoboletum* var. *montanum* Atk. He likewise recognizes two forms in America, one growing on Hemlock (Murrill's *G. Tsugae*), which he designates *G. pseudoboletum* var. *Tsugae* Atk., and a second one found on other hosts, but especially hardwoods, which he calls *G. pseudoboletum typicum*, though probably not the typical *G. lucidum* of Europe. Murrill at first considered *G. lucidum*, the typical European form, which he preferred to call *G. pseudoboletus*, to be represented in America (11) and reported it as occurring on Oak, Alder, Hazel, Maple, Willow, Honey Locust, Sweet Gum, and Beech, throughout Europe, and in England, Australia, and America. In his later work (12) (13) reference to the species is omitted, and although we do not know what disposition was made of the numerous American collections previously reported by him, we must believe that Murrill came to the conclusion that the American forms were distinct, and that *G. lucidum* does not occur in America. Overholts (15), voicing a third viewpoint, believes that *G. lucidum*, which he calls *Polyporus lucidus*, is an American as well as a European species, and that it is found generally throughout the eastern part of the United States on the trunks and roots of deciduous trees. He does not recognize it, however, as occurring on conifers; for such he adopts Murrill's name *G. Tsugae* (*Polyporus Tsugae*), though with wider significance (15).

The American authorities are likewise almost as far apart in their notions of habit, shape, and color, as in the matters of name and hosts. This has naturally followed from the circumstance that there has been no agreement as to the limitation of the species, and

also because there has been so often no clear differentiation between variable and constant characters.

(b) *Ganoderma sessile* Murr.

This species was originally described by Murrill (11) as a sessile form occurring on deciduous trees. It was stated to differ from *G. lucidum* in having an acute margin, a more rugose surface and in being always without a stipe. This first description was subsequently much modified, so that in "Northern Polypores" (13) we find *G. sessile* described as either sessile or laterally stipitate, and as occurring on conifers or hardwoods. From the later descriptions of this species we gather that the characteristic features of the fruit body are its reddish chestnut color, more or less zoned surface, an acute margin and a fibrous context. The author states that it resembles *Polyporus lucidus* of Europe, but considers that *G. sessile* is an indigenous American plant. Overholts (14) considers it synonymous with *G. lucidum*, and Atkinson makes no mention of it. It is appropriate to refer here to *Ganoderma subperforatum* Atk., which was described by Atkinson in 1908 on the basis of a single specimen collected in Ohio. Having become impressed with the peculiar structure of the spore in *Ganoderma*, it was noticed that in this specimen the walls were relatively thin and the echinulations of the endospore reduced. This feature, and also the fact that although stipitate the occurrence was on Oak led Atkinson to consider it a hitherto undescribed species. When Murrill revised *G. sessile* so as to include stipitate forms, he considered *G. subperforatum* as probably identical. Overholts, on the other hand, considers it identical with *Polyporus lucidus*. After studying the type specimen, a privilege extended through the courtesy of the custodian of the Atkinson Herbarium, I have no hesitation in expressing agreement with Murrill's disposition of it. It is a *Ganoderma sessile*.

(c) Murrill's *Ganoderma Tsugae*

The chief characteristic of *Ganoderma Tsugae* Murr. that sets it apart from other species of *Ganoderma*, according to its author, is its host specificity for Hemlock. There are other characters noted, to be sure, but they are not of the same determinative value. In comparison with the later descriptions of *G. sessile*, the significant features seem to be a darker colored, non-zonate top, a softer context, perhaps a less acute margin, and a concave rather than a convex lower surface. Atkinson recognizes *G. Tsugae* simply as a form of *G. lucidum*. He states that in color and other characters it differs but slightly if any from the typical form, and only its host specificity



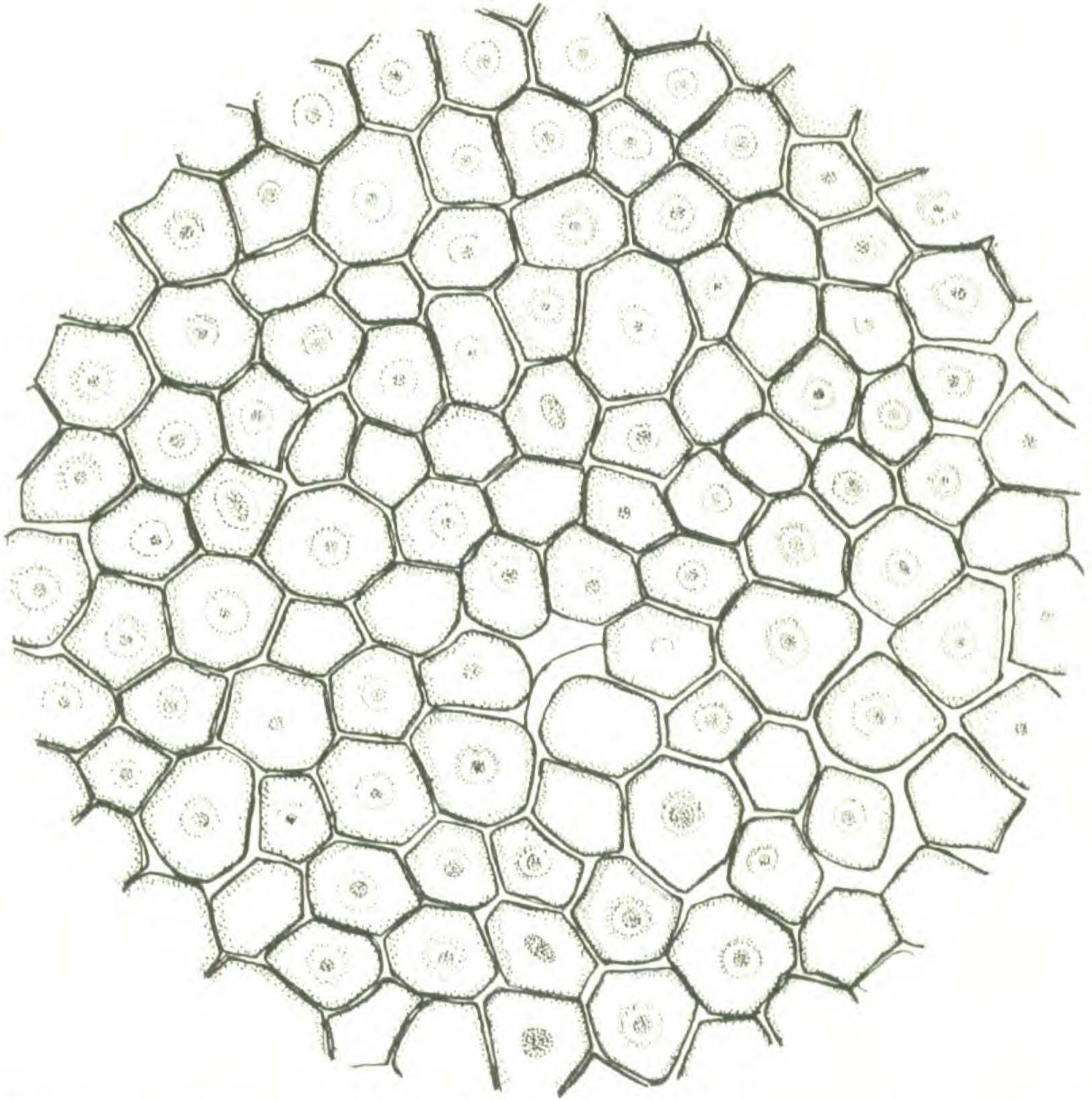
distinguishes it. According to Overholts (15) on the other hand, *G. Tsugae* cannot be differentiated by host affiliation alone, as it is found growing on and about the stumps of Pine as well as Hemlock. Overholts considers this a good species, however, recognizing in the context a distinctive structure and color and manner of branching of the hyphae, all of which, it is held, are characteristic of this form only, and serve to distinguish it from its close allies. The present writer can confirm this only in part. All the specimens which he has examined from Hemlock do display a context which in macroscopic and microscopic features answers to the description by Overholts, but many of the European collections of *G. lucidum* have these same characters, and cannot be distinguished on this basis. Similarly among Professor Faull's collections is a specimen from an oak stump which has the typical context of *G. Tsugae*, and in the herbarium of the New York Botanical Garden there is a collection from a maple log which cannot be distinguished from *G. Tsugae*, and which in fact is labelled such. Although as far as is known the specimens on Hemlock have always the same kind of context, this by no means serves to separate them from all other species.

In view of the obvious confusion which exists in regard to these species, one is led to seek an explanation. The writer believes that it is due at least in part to the assumption of host specificity, and the recognition of species on this basis. This assumption is not supported by proof. It is of course true that in the case of many of the Polypores certain hosts are favored, but in this group one is hardly justified in characterizing a species as host specific. Whether in certain species there are biological strains in which strict host specificity is developed is a possibility which in this group still remains to be demonstrated. One must, therefore, rely as yet on morphological characters alone as the basis on which species are to be recognized, and these possibilities are by no means exhausted in the case of the species under discussion. Important morphological differences are to be found in the crust and in the spores. They will probably also be found in the mycelial mats of pure cultures grown on artificial media.

#### CRITICAL STUDIES OF THE CRUST

In order to study the structure of the crusts of the sporophores, it was found necessary to prepare vertical and transverse sections. Since the varnish which covers the mature fruit body as a thin fragile pellicule dissolves rapidly in alcohol and xylol, the usual embedding methods could not be employed. The best sections showing the varnish were prepared by infiltrating with a soap solution

small blocks of the crust capped context under a reduced pressure. The material was embedded in soap, the water being evaporated off as rapidly as possible. Soap solution will gradually dissolve the varnish, but if the infiltration and embedding are done rapidly good sections can be secured. The temperature must not be high, otherwise the varnish will be melted.



Transverse section through the palisade elements of the crust of *G. oregonense* ( $\times 800$ ).

Though showing considerable specific differences, the crusts of all our *Ganodermas* have certain features in common. They are seen to be composed of the enlarged and somewhat bulbous ends of hyphae growing out from the context. These are arranged very compactly together in the vertical position; and they form a sort of palisade layer, over the surface of which is the hardened varnish, resembling a thick fragile cuticle. The hyphal elements which together compose the crusts are typically very thick walled, and appear to be impregnated with the dark orange varnishing substance

which they have secreted. In cross section they are angular, frequently pentagonal or hexagonal, and are surprisingly uniform in shape and size. They are without surface pores, and it is only with difficulty that a central canal or lumen can be made out. The walls appear to be thickened concentrically, until the elements are practically solid. Their color is a rich orange yellow, which penetrates uniformly to a depth somewhat below that of the base of the palisade layer into the thick-walled threads of the context. In very thin sections the color is faint yellow.

(a) **Ganoderma oregonense** Murrill

This species has a crust which is darker in color, thicker, and of more regular structure than the crust of any other species studied. The club-shaped elements of which it is composed are from 50 to 60  $\mu$  in length and from 6 to 10  $\mu$  in diameter. In thin sections the color, which is orange yellow, is seen to penetrate from the surface to a depth of as much as 275  $\mu$ . In specimens which have developed favorably the varnish may be 15  $\mu$  thick. See Fig. 16.

(b) **Ganoderma lucidum** (Leys.) Karst.

In the case of this species, which is taken to include *G. Tsugae* Murr., the crust differs from that of *G. oregonense* only in being composed of slightly shorter bulbous elements, which are sometimes not as regularly arranged, and in having a thinner coat of varnish. In *G. oregonense* the hyphae approaching the crustal layer are rather straight and uniform, while in *G. lucidum* they are usually crooked, tangled, and of varying diameter. This feature in *G. lucidum*, however, is by no means constant. The character of the crust is doubtless determined to some considerable extent by the nature of the conditions under which the sporophore comes to maturity. In *G. lucidum* the bulbous elements of the crust are about 40  $\mu$  long, and from 6 to 8  $\mu$  in diameter. The varnish is commonly about 12  $\mu$  thick. The crust of a typical *G. lucidum* is illustrated in vertical section in Fig. 8.

(c) **Ganoderma Curtisii** Berk.

This species is usually described as partially varnished or with varnish coming off in flakes. An examination of the crust reveals the interesting fact that the whole of the palisade layer exfoliates leaving the sporophore with a chamois-like surface of densely woven fine hyphal ends. The crust of this species is comparatively thin. The palisade elements are bulbous and commonly from 15 to 25  $\mu$  long. They arise from a stratum of densely woven fine hyphae, which constitutes a plane of weakness along which the separation

of the crust from the sporophore takes place whenever the former is shed in irregular flakes. Not infrequently there are thin-walled elements, such as are observed at the growing margin of all species, interspersed among those with thickened walls. This feature is one never observed in other species. Spores may be found embedded in the crust. In *G. Curtisii* the total thickness of the crust including the varnish is about 30  $\mu$ . See Fig. 18.

(d) *Ganoderma sessile* Murrill

In *G. sessile* the crust is distinctly different from that of other species. The palisade elements are bulbous rather than club shaped and, although forming a dense compact stratum, are not as closely and uniformly fitted together as in the case of *G. lucidum* or *G. oregonense*. The crust is thinner than in those species, the bulbous elements being from 15 to 30  $\mu$  in length. The coating of varnish is distinctly thinner, being about 8  $\mu$  in depth. See Fig. 12.

#### CRITICAL STUDIES OF THE SPORES

The spores of *Ganoderma* differ from those of most of the other Polypores not only in being brown in color, but in appearing to be rough or warty superficially. Actually, they are smooth, but the peculiar structure of the walls lends an appearance of roughness, so that in the early descriptions they were described as warty, rough, echinulate, or spiny. Patouillard was the first to draw attention to the double wall of the spore, the inner of which was described as being echinulate and comparatively thick, the outer as thin, and "moulded exactly on the points of the endospore." More careful observations have shown this description to be not entirely correct. It was Atkinson (2) who first pointed out that the exterior surface of the spore wall is perfectly smooth. His deductions, however, as to the structure and development of the walls, although not stated in positive terms, were erroneous in that, not conceiving of the wall as essentially duplex, he considered the spines or echinulations of the endospore to be extensions of the brownish spore content. White (21), referring to the similar spores of *Fomes applanatus*, observed that Atkinson's interpretation was incorrect, and stated that within an original hyaline wall a "rough coated, thick, and yellow walled endospore is formed." While the nature of the outer wall of the mature spore was not clearly described, subsequent work has shown White's interpretation to be essentially correct. It remained for Coleman (4) to describe in detail the development of the duplex wall. He found that the endospore wall originates from granules laid down on the inner margin of the episporium, that these increase in size and fuse to form a membrane which thickens